

STINGING BEHAVIOR AND RESIDUAL VALUE OF WORKER HONEY BEES (*APIS MELLIFERA*)

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Abstract.—Worker honey bees of two subspecies (*Apis mellifera mellifera* and *A. m. ligustica*) were bioassayed in the laboratory to determine their willingness to sting at various ages. Foragers returning to field colonies of both subspecies were captured, bioassayed for stinging behavior, and the sugar concentration and volumes of their nectar loads were measured. Residual value theory, which has previously been demonstrated to be a good predictor of the intensity of risky nest defense by parental birds, was used to interpret these data. Workers of the more highly defensive *A. m. mellifera* displayed residual value sensitivity in their stinging behavior, while the less defensive *A. m. ligustica* did not.

The stinging behavior of worker honey bees is the final action in a suicidal form of colony defense. A bee that stings a vertebrate typically has its barbed stinging structures catch in the vertebrate's epidermis and pull out of the bee's abdomen, killing the bee. Queen honey bees have a weakly barbed stinger (see plate 1.43, Erickson, Carlson and Garment, 1986) used only to dispatch any rival queens in a colony.

No model has previously been proposed to explain whether worker bees should sting more readily at specific ages, or be equally ready to sting throughout their adult lives. Collins, Rinderer, Tucker, Sylvester and Lockett (1980) proposed a model of colony defense that incorporated genetic and environmental variables, but not worker bee age. Kolmes (1985a, b, c) and Jeanne (1986) discussed the behavioral transition from hive to field duties in terms of the hazardous nature of foraging activities, but neither addressed stinging as an especially hazardous task.

Worker bees are nonreproductive members of insect societies, capable of performing various tasks which allow their society as a whole to produce new workers and reproductives. The evolution of this system is intimately tied to the haplodiploid nature of hymenopteran genetics, and the greater degree of genetic relatedness between a worker and her full-sisters than between a worker and her own hypothetical offspring (Hamilton, 1964). Although worker bees are not themselves reproductive, their efforts on behalf of their colony can all be thought of as helping to produce future generations of closely related individuals (Oster and Wilson, 1978; Kolmes 1986).

When worker bees are considered in the fashion just described, another body of literature exists that may help us model their stinging behavior. The intensity of nest defense by song birds has been studied in terms of the residual reproductive value of the defending parents (Curio, 1987; Curio, Regelmann and Zimmermann, 1985, 1984; Pianka and Parker, 1975; Curio, Klump and Regelmann, 1983; Windt and Curio, 1986; Regelmann and Curio, 1986, 1983). Parental birds have proven to be

most likely to engage in vigorous and hazardous defensive behavior when: there were more young to defend; as time in the breeding season progressed; as age of young increased; as number of young in second broods increased; in association with sex-specific differences in residual reproductive value; and as the expected number of neighboring mobbers increased (Curio, 1987; Regelmann and Curio, 1986, 1983; Curio, Regelmann and Zimmermann, 1985, 1984; Windt and Curio, 1986; Curio, Klump and Regelmann, 1983). When a parental bird had a lower future expectation of reproductive success, in either the current or future breeding seasons, it would tend to defend its present brood more vigorously. Present risk and future expectation of success seemed to be inversely related. Parallels exist between parental birds and sterile insect workers defending nests in which they are helping to produce closely related siblings. In both instances the possibility exists of hazardous defensive behavior being related to an individual's residual value. At a moment of crisis containing the potential for self-sacrificial defensive behavior, the balance between the benefit of stinging and a worker bee's future value to the colony may govern individual behavior.

Residual value theory predicts that a worker bee should be more likely to sting when its anticipated future value to its colony is lower. We predict therefore that (a) bees should sting more readily as they age and possess shorter future life expectancies. We can also predict that bees should sting more readily when they are able to perform less work for their colony. It is difficult to quantify the work a bee performs within the hive, but a forager that is harvesting a richer floral resource should be of greater value to a colony than a forager harvesting a poor resource.

Worker bees typically develop constancies to a single type of flower. Honey bees are known to shift from one source of forage to another due to experimental manipulations of sucrose concentrations in feeders (Seeley, 1986) or natural declines in previously exploited nectar sources (Ribbands, 1949). However, a variety of evidence points to a typical flower constancy in an individual forager unless environmental conditions change considerably during its relatively brief foraging life. Workers that develop an initial attraction to one variety of apple blossom continue to forage at that variety so long as it retains its relative attractiveness, despite the presence nearby of other varieties representing more abundant floral resources (Free, 1966). Individual flowers within patches in the temperate zone have a great enough longevity in spring or early summer (ca. 5 to 7 days, Primack, 1985) that the retention of attractiveness of a species is a likely condition. Learning curves of bees trained to feeders are unaffected by wide ranges of concentrations or availabilities of sugar solutions during the first few rewards (Menzel, Erber and Masuhr, 1974; Menzel and Erber, 1972). Bees trained to artificial floral arrays develop constancy to wavelengths of floral reflectance (Jones, Scannell, Kramer and Sawyer, 1986). Constancy of foraging bees to specific flower colors has been identified as strong enough to serve as a pre-pollination isolating mechanism between species of *Cercidium*. The average "mistake frequency" of honey bees was 5.63% when two different UV floral patterns were presented, despite nearly equal caloric rewards presented by different species of *Cercidium* (Jones, 1978). Other experiments have shown that food odor is entrained to even more strongly by honey bees than flower color (Free, 1970). The actual foraging area returned to by individual worker bees has been shown to be quite small (Ribbands, 1949; Free, 1966; Levin, 1966). Bees are most constant to floral sources that

supply both nectar and pollen (Ribbands, 1949). Most foragers are constant to one type of pollen (Sekiguchi and Sakagami, 1966; Free, 1963). Pollen constancy tends to be retained even when a colony is moved to a new location, and under circumstances where different pollen sources become available at various times of day (Free, 1963). Other data providing evidence of flower constancy that are too numerous to cite are presented in Grant (1950), and Wells and Wells (1983).

The preceding material points to a great potential for flower constancy in the foraging behavior of most honey bees. Workers tend to remain constant to the resource they initially begin to exploit, and bees develop preferences for floral resources within a wide range of acceptability. The variability of floral resource value, and the likelihood that a bee will continue to exploit one resource unless it deteriorates considerably, leads to our second prediction about honey bee stinging behavior and residual value. We predict that (b) foragers returning to their colony with less valuable nectar loads might be expected to sting more readily than more "valuable" foragers.

The experiments were performed to test predictions (a) and (b). In one, we individually measured the threshold stimulus required to elicit stinging for worker bees of known ages using a laboratory bioassay. This was done for workers from colonies of two subspecies of honey bees, British bees (*Apis mellifera mellifera*) and Italian-derived bees (*A. m. ligustica*). In a second series of experiments we captured foragers as they returned to colonies, and measured their threshold stimulus to elicit stinging as well as the volume and sugar concentration of nectar in their honey stomachs. The latter experiments allowed us to ask whether or not foragers were modifying their stinging behavior on the basis of the value of the nectar load they carried.

MATERIALS AND METHODS

This research was conducted at the Bee Research Unit of University College, Cardiff, Wales. Two colonies of honey bees were used in the experiment, one of dark British honey bees (*Apis mellifera mellifera*) and the other light Italian honey bees (*A. m. ligustica*). The Italian bee colony had been established using a mated queen imported from New Zealand. The colonies were each possessed of the distinctive behavioral traits typical of their respective subspecies. The Italian bees were "gentle" and the "highly defensive" British workers were much more prone to emerge rapidly from the hive when disturbed, and to attack and sting in the apiary more readily and persistently than the Italian colony. When the defensiveness of British and Italian colonies in our apiary was measured by bouncing a black suede ball at their entrances (Free, 1961) the British colonies had a shorter latency to delivery of the first sting than the Italian bees (avg. of 3.5 sec vs. 17 sec), the British colonies delivered more stings to the suede ball in the first minute of the test (avg. of 39.5 stings vs. 2 stings), and the British bees continued to attack the suede ball when it was withdrawn further than did the Italian bees (avg. 6.3 m vs. 2.5 m) (Echazarreta and Paxton, unpublished data). Each colony fully occupied one deep British standard hive body and filled most of one shallow hive super above it for honey stores, and contained healthy levels of eggs and brood throughout the experiment.

Experiment I. Frames of capped brood ready to emerge were removed from both colonies and placed overnight in an incubator at 32–34°C. The newly emerged workers were collected the following day, marked, lightly sprayed with sugar syrup, and reintroduced into their colonies of origin. The Italian colony received 842 marked

workers, and the British colony received 504 marked workers. All 1,346 bees were returned to their natal colonies on the same day in order to prevent environmental variables that fluctuate from day to day from affecting the experimental bees differently. One hundred of the workers placed in each colony were individually marked on their thoraxes with colored and numbered tags. The other marked bees were color-coded with ink on their thoraxes as an age cohort.

Workers were removed from the colonies at intervals to test for their willingness to sting. The intervals were irregular because the colonies were not sampled during rainy periods, and because of an intentionally long period at the end of the experiment so that bees well into their foraging lives could be tested. An initial 4 day period was given for workers to be accepted and acclimated to their colonies. Twenty British and 20 Italian bees were then removed from their colonies at 5, 7, 10, 12, 14, 18, 20, 21, 24 and 31 days of age.

Workers were tested for their willingness to sting by being gently removed from their colony with forceps, placed individually between the lid of a small plastic petri plate (57 mm diameter) and a 7.6 cm × 12.7 cm index card, and allowed to remain there for several minutes until there was no apparent disturbance among them. Each petri plate assembly and bee in turn was then gently transferred to the test apparatus, and the index card was slid out from beneath the bee. The new surface that the bee stood on consisted of a grid of parallel steel wires of approximately 2 mm diameter and 3.5 mm interwire spacing. Under the wires was a floor consisting of a prewashed black suede target. Each suede target was used for testing one bee, removed, and washed and aired for at least a day before being used on subsequent trials. Testing bees individually allowed us to avoid the type of group-size effect known in metabolic responses to alarm pheromones (Southwick and Moritz, 1985; Moritz, Southwick and Breh, 1985; Moritz and Burgin, 1987).

The wires were arranged so that they alternated positive and negative polarity. A bee standing on any two adjacent wires completed a circuit. The positive and negative connections ran to a Coutant 200.2 DC power supply. A potential difference between the positive and negative wires beginning at 0 volts was increased by 1 volt per second whenever a bee was in contact with two adjacent wires. One observer watched the bee to determine when contact was being made, and a second observer slowly increased the voltage whenever it was appropriate to do so. The maximum current flow through the system was preset at 50 milliamps. The individual bees were free to climb onto the wall or ceiling of the petri plate lid, groom themselves, and generally to behave naturally within the limits of their confinement. This ability of the bees to move off of the flooring lengthened the time required to test each bee considerably, but it was felt to be compensated for by the more natural behavior that it allowed.

At some point a threshold voltage was reached and the test bee suddenly stung downwards into the suede target with a characteristic flexion of its abdomen and a braced stance. This stinging posture was identical to the typical stinging behavior familiar to anyone who has worked with honey bees. A total of 400 known-aged bees (200 British and 200 Italian) were tested using this procedure. Worker bees sting more readily in defense of their hive than at flowers, and they are attracted to sting by dark colors and coarse surface textures (Free, 1961). In these regards, presenting a black suede target to a bee collected at its colony provides a good representation of the situation present when a bee defends its hive from a (typically) dark-colored

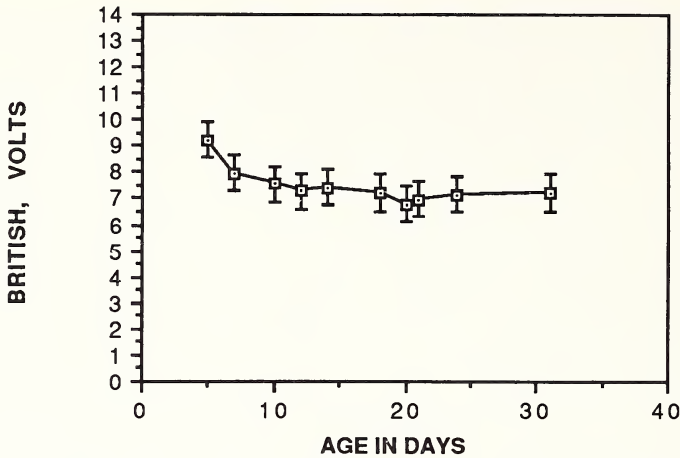


Fig. 1. Threshold stimuli required to elicit stinging behavior in the British subspecies, *Apis mellifera mellifera*. Values are expressed as means with standard deviation bars. A total of 200 bees were bioassayed at the various ages indicated.

mammalian threat. See Kolmes and Fergusson-Kolmes (in press) for further description and discussion of this method.

The age at which workers began foraging was determined by observing the hive entrances. Observations were carried out at worker ages of 3, 5, 7, 10, 12, 14, 18, 20, 21, 24, 27, 28, and 31 days. Irregular sampling intervals were due to variable weather, with observations not being carried out on rainy days in order to avoid humidity effects (Collins, 1981). Entrances were blocked with a wire screen for 15 min and then observed for an additional 15 min while the entrances remained blocked. The first foraging trip was considered to be the date that an individually marked worker was initially seen outside the hive during entrance observations. Although a small number of these flights may have been orientation flights rather than foraging flights, previous studies have indicated that error due to this factor is not significant (Winston and Katz, 1982; Winston and Punnett, 1982; Winston and Fergusson, 1985, 1986; Fergusson and Winston, 1988).

Data were analyzed using Wilcoxon matched-pairs signed-ranks tests, Chi-squared 2×2 contingency tests corrected for continuity, Mann-Whitney U tests, Kruskal-Wallis one-way ANOVAs, and Chi-squared tests for two independent samples (Siegel, 1956). All of these are nonparametric statistics that do not make the assumptions of normal distributions or homogeneity of variance among the data sets.

Experiment II. Workers returning to the Italian (48 bees) and British (48 bees) colonies were captured with forceps, and individually isolated. Only foragers returning to their colony without pollen loads were collected, because of the considerably increased difficulty in evaluating the worth of simultaneous pollen and nectar loads. The bees were tested for their threshold voltages required to elicit stinging as already described. After this procedure, bees were rendered unconscious with carbon dioxide, and the contents of their honey stomachs were drawn from their mouths into a micropipette by pressure on their abdomen (Gary and Lorenzen, 1976) followed by

dissection to ensure that all of the contents had been gathered. The difference between capturing these workers as they alighted at the hive entrance, and removing workers from frames within the hive in Experiment I, precluded direct comparisons of threshold voltages measured in the two experiments.

The volume of each honey stomach's contents was measured by determining what portion of a micropipette's length was filled (4 cm = 20 microliters). Sugar concentration of each honey stomach's contents was measured in sucrose equivalents with a refractometer.

Data were analyzed in order to examine the relationship between the value of the nectar load being brought back to the colony and the threshold stimulus required to elicit stinging. The data were analyzed 3 ways, as threshold stimulus vs. (a) microliters being carried, (b) micrograms of sucrose equivalents per microliter in the honey stomach contents, and (c) total micrograms of sucrose equivalents in the nectar load (concentration \times volume). A fourth analysis compared the volume of nectar loads to their concentration in sucrose equivalents, to see whether bees were discriminating in their foraging as might be expected (Schmid-Hempel, Kacelnik and Houston, 1985; Wells and Giacchino, 1968; Seeley, 1986). Bees with empty honey stomachs were often foragers marked visibly with *Impatiens* pollen, but with no nectar load at the moment of capture. These empty bees were excluded from analyses involving nectar concentrations. Kendall Rank Correlation Coefficients (Siegel, 1956) were used in data analysis.

RESULTS

Experiment I. Stinging behavior measurements for individual workers of the two subspecies of honey bees differed in a fashion consistent with the dark bouncing suede ball test results already mentioned. British bees stung at lower threshold stimulus levels than Italian-derived bees, with very significant differences between them when data from both colonies at every age date were compared with a Wilcoxon matched-pairs signed-ranks test (sum of less frequent ranks = 0, $P < .005$) (Figs. 1, 2). British bees were, overall, more defensive.

The stinging behavior of each subspecies of bee varied with age. Italian bees had threshold stimuli required to elicit stinging ranging from 10.88 ± 2.38 volts (mean \pm standard deviation) at 5 days of age to 7.60 ± 1.87 volts at 18 days of age (Fig. 2). British bees had threshold stimuli required to elicit stinging range from 9.23 ± 3.50 volts (mean \pm standard deviation) at 5 days of age to 6.80 ± 1.70 volts at 20 days of age (Fig. 1). The overall picture for both subspecies is of an initially declining threshold stimulus required to elicit stinging, to a minimum value around 18 or 20 days of age. British bees demonstrated only a slight increase in threshold stimuli required to elicit stinging after this age, up to 7.23 ± 2.25 volts at 31 days of age. Italian bees showed a considerably greater rebound in their threshold stimuli required to elicit stinging, reaching 10.43 ± 3.16 volts at 31 days of age. Both British and Italian bees therefore were less likely to sting when young, and became more likely to sting at intermediate ages. Only the Italian bees subsequently became considerably less likely to sting as they aged further.

The age at which worker bees demonstrated their greatest willingness to sting coincided with the period immediately prior to their average age of first foraging. British bees had an average age of first foraging of 20.52 ± 6.39 days (mean \pm

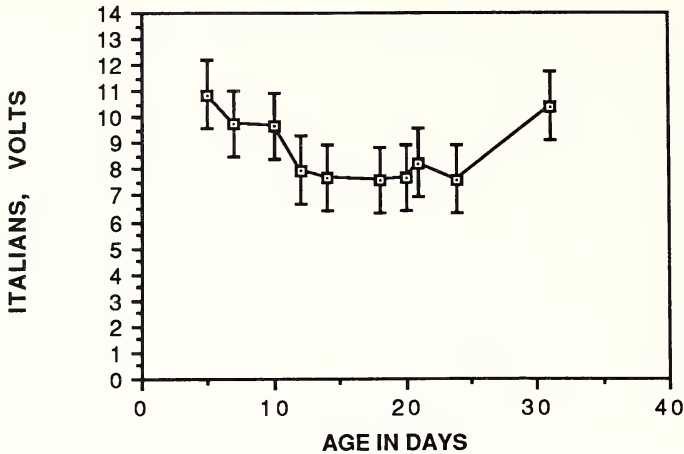


Fig. 2. Threshold stimuli required to elicit stinging behavior in the Italian subspecies, *Apis mellifera ligustica*. Values are expressed as means with standard deviation bars. A total of 200 bees were bioassayed at the various ages indicated.

standard deviation) while Italian bees began to forage at 20.03 ± 5.60 days of age. When the first foraging ages for the 56 bees for which data was collected were categorized according to their subspecies and compared using a Mann-Whitney *U* test, the ages of first foraging for representatives of the two subspecies did not differ significantly from one another ($U = 315$, $P = .3734$, 2-tailed test).

In order to determine whether the age-related variability of threshold stimuli required to elicit stinging in both British and Italian bees was significant, data for each subspecies were analyzed separately using a Kruskal-Wallis one-way analysis of variance. This approach asked whether the differences between the samples (threshold data for different ages) for each subspecies were great enough to indicate that they were drawn from different populations (i.e., if bees of the same subspecies at different ages demonstrated significantly different threshold stimuli for stinging). For both British and Italian bees, the age-related differences proved to be significant. The one-way ANOVA results for British bees were H (adjusted for ties) = 17.11 ($P < .05$, 9 degrees of freedom). The one-way ANOVA results for Italian bees were H (adjusted for ties) = 46.03 ($P < .001$, 9 degrees of freedom). Both British and Italian bees did vary significantly in their likelihood of stinging according to their age.

Experiment II. The British and Italian bees proved to be similar in two regards in the relationships of their stinging responses to the characteristics of the nectar loads they were bearing back to their colonies. First, neither type of forager demonstrated a significant association between their threshold stimulus to elicit stinging and the concentration of their nectar load in micrograms of sucrose equivalents per microliter (Fig. 3) ((a) British bees: Kendall Rank Correlation Coefficient = .1530, $P = .1131$, $N = 31$, 1-tailed test; (b) Italian bees: Kendall Rank Correlation Coefficient = $-.1010$, $P = .2266$, $N = 28$, 1-tailed test). Second, both types of forager demonstrated a significant positive association between the volume of their nectar load in microliters and the nectar concentration in micrograms of sucrose equivalents per

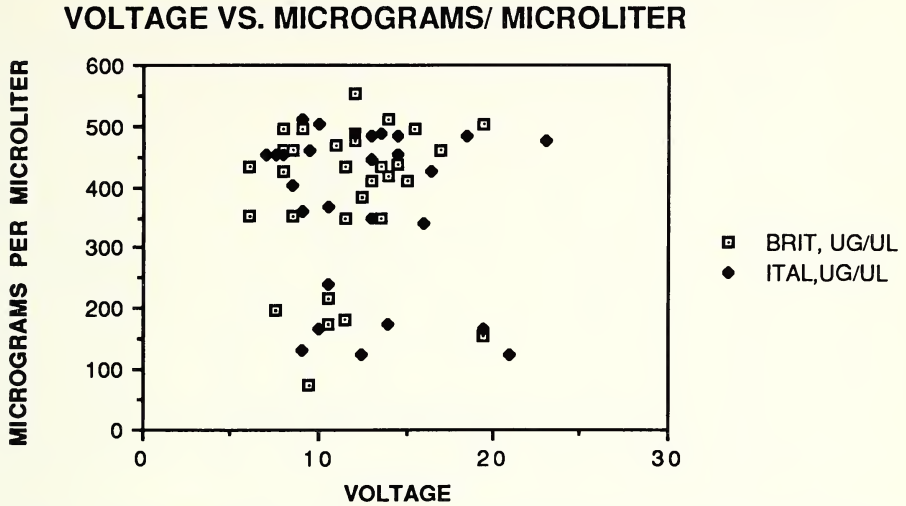


Fig. 3. Threshold stimuli required to elicit stinging behavior for two subspecies of foragers, plotted with respect to the concentration of nectar in their honey sacs expressed as micrograms/microliter of sucrose equivalents.

microliter (Fig. 4) ((a) British bees: Kendall Rank Correlation Coefficient = .2776, $P = .0143$, $N = 31$, 1-tailed test; (b) Italian bees: Kendall Rank Correlation Coefficient = .3184, $P = .0087$, $N = 28$, 1-tailed test). The foragers did not modify their stinging behavior due to differences in micrograms of sucrose equivalents per microliter of nectar borne by them. The foragers did gather a greater volume of more concentrated nectar, demonstrating the expected discrimination.

The British bees displayed stinging behavior that varied with their nectar loads in two significant fashions. There was a significant positive association between threshold stimuli required to elicit stinging and total micrograms of sucrose equivalents carried (Fig. 5) (Kendall Rank Correlation Coefficient = .1919, $P = .0274$, $N = 48$, 1-tailed test). There was also a significant positive association between threshold stimuli required to elicit stinging and microliters of nectar carried (Fig. 6) (Kendall Rank Correlation Coefficient = .1895, $P = .0287$, $N = 48$, 1-tailed test).

The Italian bees differed by not demonstrating a significant association between threshold voltage required to elicit stinging and either total micrograms of sucrose equivalents carried (Fig. 5) (Kendall Rank Correlation Coefficient = .0833, $P = .2005$, $N = 48$, 1-tailed test) or microliters of nectar carried (Fig. 6) (Kendall Rank Correlation Coefficient = .0520, $P = .3015$, $N = 48$, 1-tailed test). British bees therefore appeared to modify their stinging behavior in terms of their foraging success in significant ways that Italian bees did not.

DISCUSSION

Residual value theory has proven to be a useful model to predict changes in the stinging behavior of some honey bees. Workers from the colony of British bees (*Apis*

MICROLITERS VS MICROGRAM/MICROLITER

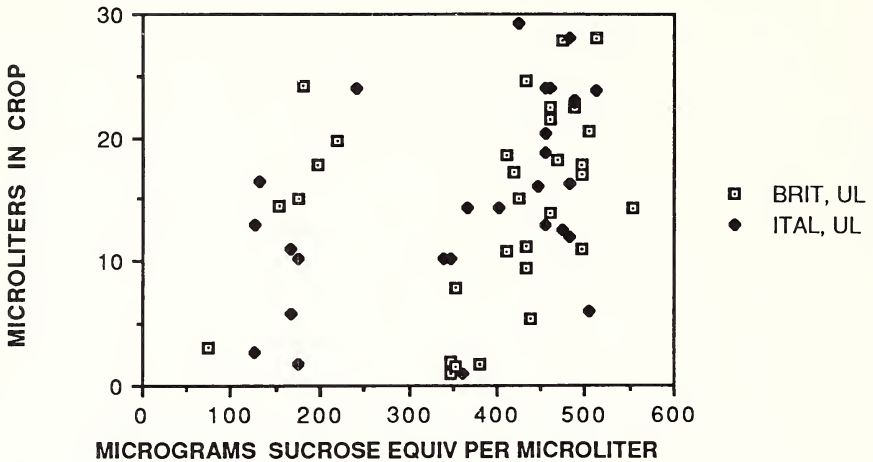


Fig. 4. The volume in microliters of nectar loads carried in the honey sacs of two subspecies of foragers, plotted with respect to the concentration of nectar in their loads expressed as micrograms/microliter sucrose equivalents.

mellifera mellifera) appeared to sting in a residual-value sensitive fashion in two ways: (a) they sting more readily when carrying fewer microliters of nectar, and (b) they sting more readily when older than approximately 10 days of age (Figs. 1, 6). The significant positive association between threshold stimuli to elicit stinging and total micrograms of sucrose equivalents carried (Fig. 5) is probably a function of the relationship already mentioned between threshold stimuli and microliters carried, because total micrograms of sucrose equivalents are calculated in part on the basis of microliters carried. There was no independent evidence that workers of this subspecies modified their stinging behavior on the basis of the concentration of their nectar loads alone (Fig. 3).

In contrast, Italian bees (*Apis mellifera ligustica*) displayed none of the modifications of their readiness to sting that are consistent with residual value theory. They possess a high threshold stimulus to elicit stinging at an advanced age (Fig. 2) and have no significant associations between stinging behavior and either nectar load size, concentration, or total net load (Figs. 3, 5, 6). The workers of this subspecies were both less willing to sting overall and appeared to be less residual value sensitive than the workers of *A. m. mellifera*.

Increased locomotion and wing flicking among groups of caged bees presented with alarm pheromones (Collins, 1980), electroantennagram responses to alarm pheromones (Allan, Slessor, Winston and King, 1987), and increases in oxygen consumption among groups of caged workers exposed to alarm pheromones (Moritz, Southwick and Breh, 1985) have all been used to examine how groups of bees of various ages react to chemicals released when a hive is threatened. In all instances the bees reacted more strongly at intermediate ages than immediately after emergence, and

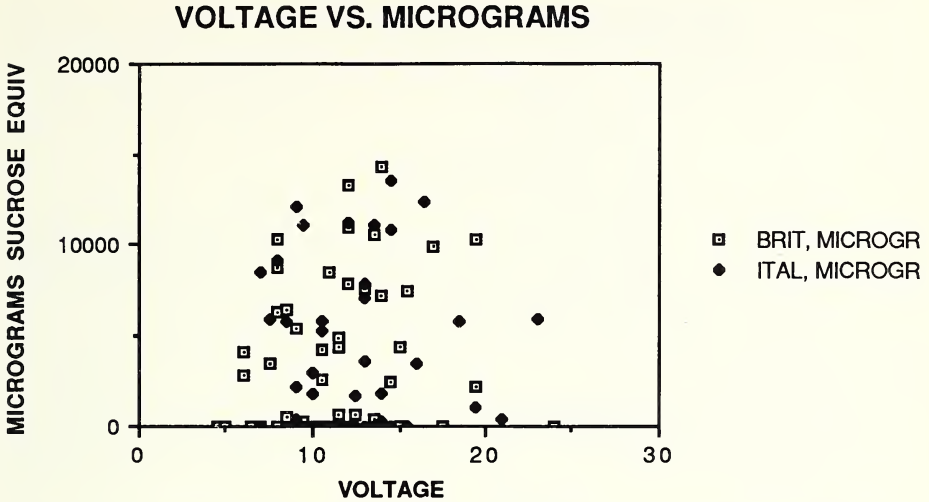


Fig. 5. Threshold stimuli required to elicit stinging behavior for two subspecies of foragers, plotted with respect to the total amount of carbohydrate in their honey sacs expressed as micrograms of sucrose equivalents.

reactivity either reached a plateau or subsequently declined. These group data are consistent with the sorts of stinging response measures reported in our data.

Both the British and Italian workers were significantly more likely to collect larger nectar loads when foraging at more concentrated floral resources (Fig. 4). This is consistent with what we know about the sensitivity of honey bees in general to varying environmental resources (Schmid-Hempel, Kacelnik and Houston, 1985; Seeley, 1986). Workers of the two subspecies also began to forage at the same age, which is consistent with data suggesting that foraging onset is controlled in part by sensitivity to environmental circumstances (Kolmes, 1985a). Apparently British and Italian bees differ from one another in their stinging behavior, but not in their foraging behavior in the manner of European vs. Africanized bees (Winston and Katz, 1982).

The significant positive association between the size and concentration of nectar loads for bees foraging on natural floral resources (Fig. 4) is consistent with reports by von Frisch (1934, 1965, 1971) that workers collect larger nectar loads from artificial feeders when the sucrose solution is more concentrated. Both the data collected from foragers on natural floral sources (Fig. 4) and those of von Frisch (1934, 1965, 1971) are contradictory to those reported by Wells and Giacchino (1968) which showed no relationship between nectar load volume and concentration. The short distance (50 m) between hive and feeders in Wells and Giacchino's study (1968) may have resulted in more typical discriminatory foraging behavior breaking down.

To further examine honey bee stinging behavior in terms of residual value theory, a number of questions must be answered. These include: (a) How variable are different colonies of both subspecies in their stinging behavior and in its modifiability? Stinging behavior may be related to the annual colony life cycle of honey bees, especially as individual workers may be of greater value to newly founded colonies than to older

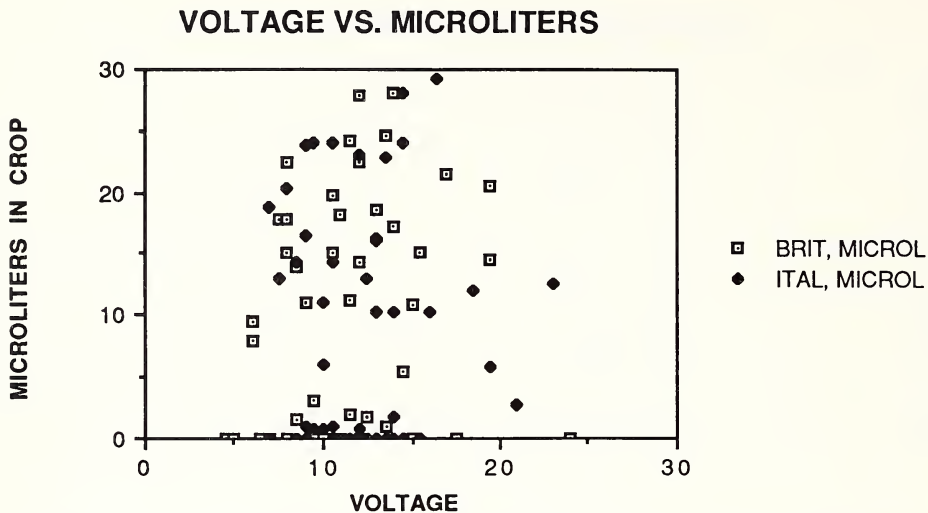


Fig. 6. Threshold stimuli required to elicit stinging behavior for two subspecies of foragers, plotted with respect to the volume carried in their honey sacs expressed in microliters.

populous colonies. (b) Do these two subspecies differ in their ages of guard duties? Although both subspecies have similar minimum threshold stimuli to elicit stinging immediately prior to their average age of first foraging, the British bees maintain approximately this level of stinging threshold while the Italian bees have a declining readiness to sting at a later age. This could be reflected by a broader age-range of guarding behavior among *A. m. mellifera* workers, if threshold stimuli required to elicit stinging are motivationally related to guarding behavior. (c) Is there any influence of the value of a floral resource in terms of pollen on stinging behavior? The data presented in this paper dealt only with nectar foragers because of the difficulties inherent in quantifying the values of pollen loads or of mixed pollen and nectar loads. (d) Would data that included more information about foraging workers (e.g., distance to floral resources; numbers of round trips per hour; precise ages of workers; amount of competition for resources with workers from other colonies; worker life expectancy) demonstrate a stronger residual value sensitivity for workers of either subspecies? (e) Are workers of additional subspecies of honey bees, such as Africanized bees, sensitive to their residual value in their stinging behavior? (f) Do workers of other social insects possess residual value sensitivity in their defensive behavior?

Finally, residual value sensitivity in stinging behavior may be important to incorporate into general models of colony defense (Collins, Rinderer, Tucker, Sylvester and Lockett, 1980) for some if not all honey bee subspecies. It may be that variable behavioral responsiveness to stimuli eliciting stinging are related to sensory changes with age (Allan, Slessor, Winston and King, 1987). The relationship between readiness to sting of workers at various ages and guarding behavior (Moore, Breed and Moor, 1987) also remains to be elucidated. This first examination of stinging behavior by worker honey bees in terms of residual value theory is a small beginning compared to the more fully developed empirical evidence in the ornithological literature (Curio,

1987; Curio, Regelman and Zimmermann, 1984, 1985; Pianka and Parker, 1975; Curio, Klump and Regelman, 1983; Windt and Curio, 1986; Regelman and Curio, 1986, 1983) but it may provide a useful approach to studying and predicting the behavior of the social insects.

ACKNOWLEDGMENTS

This research was conducted at the Bee Research Unit, Department of Zoology, University College, Cardiff, Wales CF1 1XL, UK.

We thank Professor R. S. Pickard and the Bee Research Unit, of which he is Head, for so generously acting as hosts during the course of this research, R. J. Paxton and other inhabitants of the Black Box, too numerous to individually name, and Professor J. B. Free provided us with help and stimulating conversation. R. J. Paxton and C. Echazarreta supplied us with the "bouncing ball" data for the Cardiff apiary. This work was supported through a Junior Leave for SAK and other research funds provided by the Hewlett and Mellon Foundations and Hobart and William Smith Colleges. The staff of the International Bee Research Association headquarters in Cardiff kindly assisted with library resources. We thank two anonymous reviewers for their helpful comments.

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Received July 29, 1988; accepted November 5, 1988.